

REDESCRIPTION OF THE OLIGOCHAETE GENUS
PROPAPPUS, AND DIAGNOSIS OF THE NEW
FAMILY PROPAPPIDAE (ANNELIDA: OLIGOCHAETA)

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Abstract.—Examination of type material of *Propappus glandulosus* Michaelsen, 1905, and *P. volki* Michaelsen, 1916, as well as other material of the latter, led to a reconsideration of the classification of *Propappus* Michaelsen, 1905, within the Enchytraeidae. Species included in *Propappus*, *P. volki*, *P. glandulosus*, and *P. arhyncotus* Sokolskaja, 1972, possess character-states that are unique. They have sigmoid, nodulate, bifid setae; large epidermal glands posterior to each setal bundle; spermathecal pores at septum 3/4; and glandular parts of the vasa deferentia located posterior to 11/12. Another significant, unique character state is the location of the single pair of ovaries in XIII, except in *P. arhyncotus*, rather than in the male pore segment, XII. This character, in addition to the others, warrants the removal of *Propappus* from the Enchytraeidae. The new, monotypic family Propappidae is erected for species of *Propappus*. The genus *Propappus* is redefined. *Propappus glandulosus* and *P. volki* are redescribed, and a description of *P. arhyncotus* is given.

Propappus Michaelsen, 1905, has been accepted as being nearest the stem form of the Enchytraeidae (Michaelsen 1916a, 1923; Stephenson 1930; Cernovitov 1937a; Timm 1981). These authors thought that *Propappus* exhibited a high number of ancestral states for the Enchytraeidae, reminiscent of a freshwater origin of the family. All species of the genus, *P. glandulosus* Michaelsen, 1905, *P. volki* Michaelsen, 1916, and *P. arhyncotus* Sokolskaja, 1972, are known from temperate, fresh waters. The presence of both *P. glandulosus* and *P. volki* in Lake Baikal, an ancient lake, enhanced the view of the genus as, itself, relatively ancient. *Propappus volki*, the species most studied, is regarded as characteristic of pure waters with sandy bottoms, and strong or moderate currents (Bird 1982).

Michaelsen (1905) established the genus *Propappus* and described its type species (by monotypy), *P. glandulosus*. In his diagnosis of this genus he noted that one characteristic was unique for the Enchytraeidae: the setae

on all the segments were distinctly double-pointed (now see also *Barbidrilus* Loden and Locy, 1980). His species description included other character states anomalous for Enchytraeidae: 1) each setal bundle was associated with a large, glandular organ; 2) setae occurred ventrally in the male pore segment; 3) the sperm funnel was not glandular, but the ental part of the vas deferens, posterior to 11/12, was thickened and glandular; and 4) the ovary was located on the posterior of 12/13, in the segment posterior to the male pore segment. According to the latter character state the species of *Propappus* were plesiopore, like all other enchytraeids, but had a sterile segment between the two fertile segments, as in many earthworms (Lumbricida Brinkhurst, 1982) and some Haplotaxidae and Lumbriculidae.

Michaelsen (1916a, b) described a second species, *Propappus volki*. It differed from *P. glandulosus* in that it was slightly larger and possessed a well-developed, finger-like, prostomial proboscis. Michaelsen (1916a)

noted that the ectal pore of the spermatheca was anterior to the setae of IV, as ("wie auch bei . . .") in *P. glandulosus*. This was, in fact, an amendment to the original description of *P. glandulosus* in which the spermathecal pore had been described in the usual enchytraeid position, at 4/5. In his early papers on *Propappus*, Michaelsen (1905, 1916a) described the ovaries in XIII, with the egg cell string extending from 12/13, and clearly recognized (Michaelson 1905) that this was not the usual enchytraeid condition. He did not include the location of the ovaries in the diagnosis of *Propappus*. Later, Michaelsen (1923) described the ovaries in *P. volki* as lying on the posteroventral part of 11/12. He reported that he had never clearly seen the female funnel or female pore but thought that both were in 12/13. Material from the Volga River was used for these (Michaelsen 1923) amendments to the description of *P. volki*.

Michaelsen (1916a) suggested that, because of the double-pointed setae, the lack of integrity of the pharyngeal glands, the loose structure of the nephridial postseptale, and the structure of the sperm funnel (=the preseptal part of the male duct), *Propappus* was very likely near the stem form of the Enchytraeidae. Cernosvitov (1937a) stated categorically that *Propappus* was the most primitive genus of the Enchytraeidae. This, he thought, was most clearly shown by the setal form and the structure of the sperm funnels. He also suggested that a number of character states pointed to a close affinity between *Propappus* and a subgroup of *Mesenchytraeus* Eisen, 1878, including nephridial form, structure of the pharyngeal glands, development of the sperm funnel, and structure of the longitudinal muscles. Nielsen and Christensen (1959) suggested that *Propappus* was rather doubtfully placed in the Enchytraeidae at all. At no time was the diagnosis of that family amended to include the gonadal arrangement originally described in *Propappus*, nor were derived character states unifying *Propappus* with

other Enchytraeidae recognized. Instead, many of the derived character states possessed by *Propappus* are unique and those states that are shared with Enchytraeidae can only indicate some more remote common ancestor.

Materials and Methods

Cotype material was borrowed from the British Museum (Natural History). All material was examined under a compound microscope. Drawings were made with the aid of a drawing tube (camera lucida). Photographs were made using a Zeiss-Universal photo-microscope. The means of the lengths of the probosces of *Propappus volki* in different populations were compared using the two-sample *t* test for two-tailed hypotheses, all means were tested for significant difference from 0 and the samples were compared by a non-parametric Mann-Whitney U test (Zar 1974).

Propappidae, new family

Type genus. — *Propappus* Michaelsen, 1905.

Diagnosis. — As for type genus.

Distribution. — Palearctic.

Discussion. — Species of the genus *Propappus* do not exhibit apomorphies shared with other Enchytraeidae. A group Enchytraeidae, including *Propappus*, cannot be diagnosed. The few, obviously derived character states of *Propappus* do not allow an immediate, intuitive choice for the precise position of *Propappus* within the existing classifications of the Oligochaeta. A new family of Oligochaeta, the Propappidae with type genus *Propappus*, is established here for the single genus and its included species *P. glandulosus*, *P. volki*, and *P. arhyncotus*.

The family Propappidae is phylogenetically near both the Enchytraeidae and some species of Haplotaxidae (Coates MS). Those species of Haplotaxidae from which the lineage of the family Propappidae is not yet clearly resolved include *Metataxis americanus* (Cernosvitov 1939) and *M. brink-*

hursti (Cook 1975) in the recently recognized genus *Metataxis* Righi, 1985. Along with at least some Enchytraeidae, species of Propappidae are in a monophyletic lineage including *Metataxis falcifer* (Omodeo 1958). The initial implications of this are that *Metataxis* is paraphyletic. Characteristic of all these nominal taxa is the presence of a pair of testes in at least segment XI, and, with the exception of Enchytraeidae, the occurrence of paired ovaries only in segment XIII. In order to conserve a consistent taxonomy of the sistergroup Enchytraeidae, and to avoid attenuating the diagnosis of that family, the new family Propappidae is erected for the genus *Propappus*. The outgroup criterion for determining relative polarity of character states should be applied and phylogenetic analyses performed to resolve these genealogical problems.

The primary distinguishing characteristics of this monotypic family are discussed following the diagnosis of *Propappus*.

Propappus Michaelsen, 1905

Propappus Michaelsen, 1905:24–25; 1916a:51–55; 1923:37–42.—Stephenson, 1930:765–766.—Cernovitov, 1937a:264–267, 269–270, 277, 279.—Nielsen and Christensen, 1959:29–30.—Cekanovskaja, 1962:370–377.

Palpenchytraeus Michaelsen, 1916b:1; 1916a:52; nomen nudum.

Type species.—*Propappus glandulosus* Michaelsen, 1905, by monotypy.

Diagnosis.—Setae in 4 bundles per segment, including genital segments; bundles ventrolateral and dorsolateral. Three setae, rarely 2, per bundle; setae sigmoid, bifid, nodulate. Setal gland present immediately posterior to each setal bundle (Figs. 1a, g; 2a & 2b). Head and other dorsal pores absent. Prostomium with or without proboscis. Clitellum single-layered, usually extending over XII–XIV. Pores of male and female reproductive systems paired. Spermathecal pores anterolateral in IV. Male

pores (Fig. 1a, m) anterior to ventral setal bundles and setal glands of XII. Female pores ventral, in or just posterior to 13/14. Anus opening dorsally. Cavity of prostomium almost filled by elongate, glandular, epidermal cells (Fig. 1a, pg). Brain deeply cleft posteriorly, divided into almost separate, lateral lobes. Dorsal pharyngeal pad (Fig. 1a, p) slightly thickened, protrusile. Bodies of glandular cells of pharyngeal pad not organized into compact pharyngeal glands. Gut without appendages or diverticula; expansion at intestinal origin may be abrupt. Holonephridial, preseptal parts of nephridia small (Fig. 1b), including funnel only; postseptal parts lobed, with little interstitial tissue. Spermathecae paired (Fig. 1a), originating in IV, not communicating with gut; ectal duct thick-walled, aglandular; ampulla abruptly expanded, thin-walled, extending posteriad through a few segments. One pair of testes (Fig. 1a, t) ventrolateral on posterior of 10/11. Seminal vesicle (Fig. 1a, sv) unpaired, extending as far anterior as VI. Sperm funnels (Fig. 1a, sf) simple, on 11/12; vasa deferentia confined to XII, anteriorly thickened (?glandular). Atria, prostates and other copulatory glands lacking. One pair of ovaries (Fig. 1a, o) ventrolateral on the posterior of 12/13 (see *P. arhyncotus*). Female ducts simple, on 13/14 (as above).

Distribution.—Palearctic. Central and eastern USSR; England; France; Austria; West Germany; Finland; and Norway. Lakes or running waters with moderate to strong currents; in sand or gravel.

Discussion.—The Enchytraeidae can be characterized by their possession of a number of shared character states: discrete, well-developed pharyngeal glands; testes only in XI, male pores and ovaries in XII; preseptal, glandular sperm funnels in XI; dorsal setal bundles, when present, (usually) in a mid-lateral position; spermathecal pore/pores at or just posterior to 4/5; and, frequently, modified glandular structures at the penial pore.

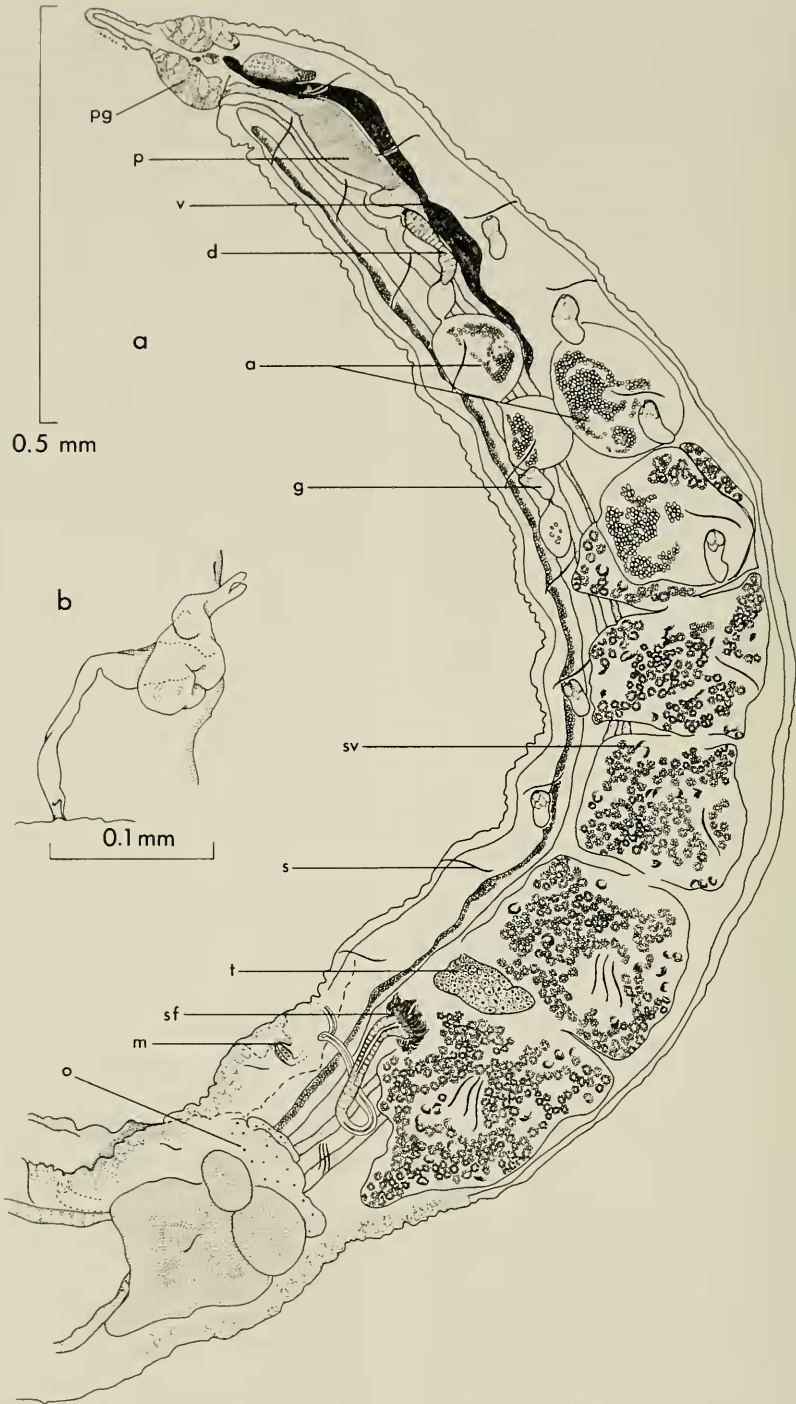


Fig. 1. *Propappus volki*: a, Drawing of anterior of whole-mount, to segment XIV; b, Nephridium from post-clitellar segment; specimens from southern England. Abbreviations—a, spermathecal ampulla; d, spermathecal duct; g, setal gland; m, male pore; o, ovary; p, pharynx; pg, prostomial glandular epidermis; s, seta; sf, sperm funnel; sv, seminal vesicle; t, testis; v, dorsal blood vessel.

The species of *Propappus* share a set of character states distinct from those of the Enchytraeidae: setae with bifid ectal ends, usually three per bundle; setal glands in association with every setal bundle; spermathecal pores at or near 3/4; thickened vasa deferentia in XII; and ovaries only in XIII with female funnels on 13/14.

The species of *Achaeta* Vejdovsky, 1877, a genus of the Enchytraeidae, lacking setae entirely, may possess sac-like organs in positions similar to those occupied by either the setal follicles of setate genera or by the setal glands of species of *Propappus*. The homologies of the organs in *Achaeta* have been debated by several authors (Michaelson 1923, Stephenson 1930, Nielsen and Christensen 1959). In megadrile and some haplotaxid oligochaetes various glandular appendages of setal follicles, which may not all be homologous structures (Stephenson 1930), have also been termed setal glands.

The organs of *Achaeta* were first described (Vejdovsky 1879) as homologues of the setae, possibly as the empty follicles. Michaelson (1923) did not think that it was possible to distinguish the setal follicles of *Achaeta* from the setal glands of *Propappus*; the organs in *Propappus* were just composed of fewer, larger cells. Thus the glands were not a unique character of *Propappus*. Both Stephenson (1930) and Cekanovskaja (1962) also saw the structures of *Achaeta* as setal glands but Nielsen and Christensen (1959) referred to these as setal follicles or setal sacs for which the true homology ("nature") was doubtful.

In sectioned and whole-mounted specimens of *Achaeta* that I have examined using a compound light microscope, cellular structure inside the cuticular sac of the setal gland could not be discerned. The contents of the cuticular sacs were granular and not densely packed. The internal cellular structure of the organs of *Propappus* is easily discernible at similar magnifications, although it does not stain with borax carmine in whole mounts. The cells of the gland do

stain with haematoxylin and are quite obvious in sectioned material. A cuticle-like outer layer can be distinguished in both whole-mounts and in sections. There appear to be two types of secretory cells present in each gland, distinguished by the stained color and by the coarseness of the granular inclusions. Such a glandular-type complement is common in invertebrate adhesive-gland systems. Cekanovskaja (1962) observed that specimens of *P. volki* adhere to stone and sand grains by means of some secretion from the setal glands of the posterior segments.

With the present information it is not possible to establish the probable homologies of the setal glands of either *Propappus* or *Achaeta*. Their distribution in *Propappus* specimens, co-occurring with all setal bundles, is unique among the microdrile oligochaetes.

Other characteristics of *Propappus* are not regarded as derived. These are the presence of unmodified, ventral setae in the male pore segment; dorsolateral location of the dorsal setal bundles; unmodified gut; diffusion of the pharyngeal gland cell bodies; and the lack of interstitial tissue associated with the postseptal part of the nephridia. These characteristics are considered "primitive" for the class Oligochaeta (Jamieson 1978; Brinkhurst 1982, 1984).

Propappus glandulosus Michaelson, 1905
Figs. 2a, 2c & 2d

Propappus glandulosus Michaelson, 1905:
25–28, figs. 4–5.—Cernosvitov, 1937b:
273–274, figs. 3–4.—Cekanovskaja, 1962:
371–272, fig. 187.

?*Propappus volki*.—Sokolskaja, 1968:21.

?*Propappus arhyncotus* Sokolskaja, 1972:
83–85, fig. 5; 1973:64–66, fig. 8.

Material examined.—Syntypes of *Propappus glandulosus*, BMNH 1949.3.1.226, mature whole-mount; BMNH 1949.3.1.227, a mature, sagittally sectioned specimen; and BMNH 1949.3.1.228, a mature, transverse-

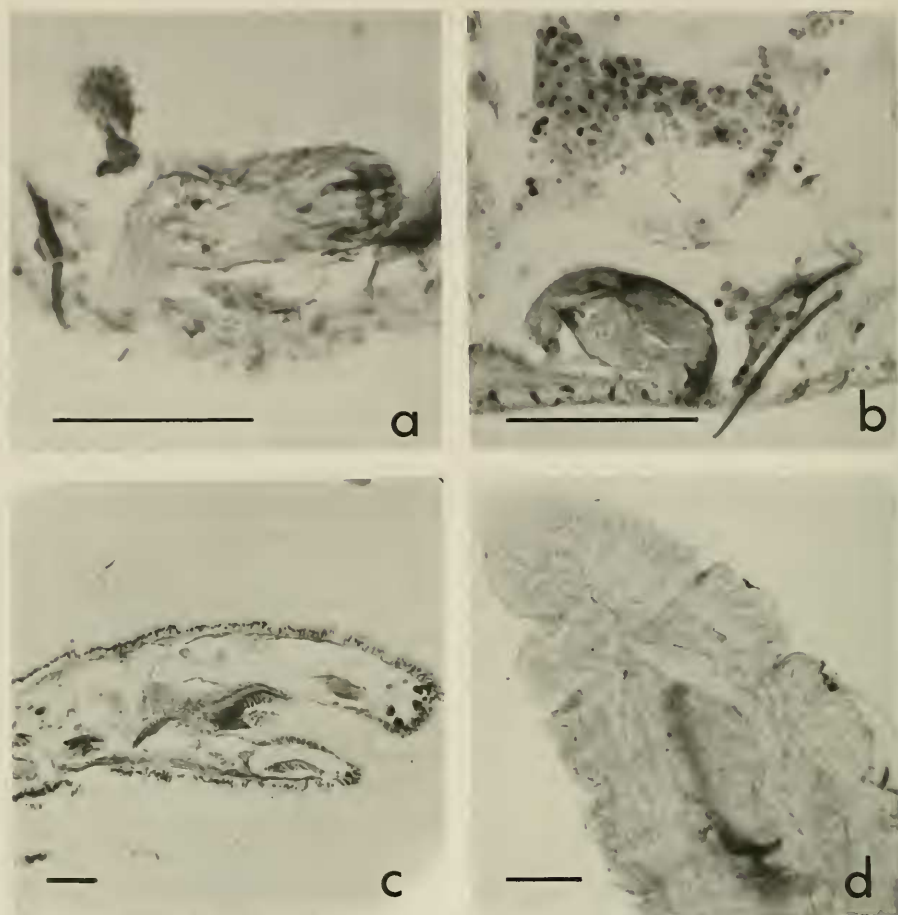


Fig. 2. a, *Propappus glandulosus*, setal gland from sectioned cotype specimen BMNH 1949.3.1.227; b, *Propappus volki*, setal gland and seta from sectioned cotype specimen BMNH 1949.3.1.230; c, *Propappus glandulosus*, sagittal section of prostomium and pharyngeal pad of cotype BMNH 1949.3.1.227; d, *Propappus glandulosus*, prostomium of whole-mounted cotype specimen BMNH 1949.3.1.226. Scale bar = 50 μm .

ly sectioned specimen. Collected in 1901 or 1902.

Type locality.—Lake Baikal, middle and southwest side, in sand or gravel at 2–8 meters depth.

Description of material examined.—Four to 5 mm long, with 28–32 segments; body diameter at IV–V (specimens slightly compressed) 175–224 (175, 219, 224) μm , at IX about 300 (301, 307) μm . Prostomium short and rounded, without proboscis (Figs. 2c & 2d). Spermathecal pores at 3/4. Setae 55–73 (59-dorsal, 55, 73-ventral) μm up to 90

μm long (according to Michaelsen 1905); nodulus in distal one-third of seta; upper tooth much shorter and thinner than lower; ventral and dorsal setae alike in size. Female pore at 13/14. Setal glands (Fig. 2a) 80, 106 μm long, 22–32 (22, 26, 32, 32) μm in diameter, flask-shaped with narrow ectal neck; entire gland appearing filled with secretions. Pharyngeal gland cells ventral in V–VIII. First pair of nephridia at 7/8 or 8/9, nephridia absent in clitellar and most of more posterior segments. Dorsal vessel origin at abrupt transition from esophagus to intes-

tine, in VIII or IX. Thick-walled ental parts of vasa deferentia about 120 μm long, 14, 24 μm in diameter; ectal part 2–3 times as long as ental, only 6–12 (6, 8, 7.5, 12) μm in diameter. Diameter of vas deferens at male pore may be slightly greater, about 13 μm , canal sometimes with short, abrupt widening just ental to pore. Spermathecal duct extending to one-half IV, ampulla extending into VI or more posteriad; duct narrowing gradually from pore to ampulla, from about 22 μm to 8–10 μm , then widening slightly at ampulla (according to Cernovitov 1937b).

Remarks.—The cotype specimens of *Propappus glandulosus* examined here came from the collections of L. Cernovitov held at the BMNH. This material was originally held in Hamburg and is from the type series (Cernovitov 1937b).

Discussion.—Although Michaelsen (1923), in redescribing *Propappus volki*, amended the position of the ovaries from 12/13 to 11/12 he did not include this characteristic in a formal generic diagnosis. In fact, *P. glandulosus* was never redescribed with the “new” ovarial position.

Michaelsen (1905) reported that the origin of the dorsal blood vessel and the abrupt widening of the esophagus to the intestine was in VIII. This was the condition seen here in *P. glandulosus* and also in the new material of *P. volki* from Lake Baikal. Further comments on the determination of the intestinal origin are made following the description of *P. arhyncotus*.

Propappus arhyncotus, also a proboscoidal, may be a synonym of *P. glandulosus*, as indicated. Three characteristics possibly distinguish the species. In *P. arhyncotus* the origin of the intestine is reported to be post-clitellar, the diameters of the vasa deferentia are greater ectally than entally, and the ovaries are located in the anterior of XII (Sokol'skaja 1972, and pers. comm.). These characteristics are discussed following the description of *P. arhyncotus*.

Distribution.—Lake Baikal, shallow (Mi-

chaelsen 1905) to abyssal (820 m) (Semernoj 1983); Yenisey River from the mouth of the Angara River to Igarka (Cekanovskaja 1962). As *Propappus arhyncotus*: Kamchatka Peninsula, Zhupanova River basin, Karymai Reach inflow to Bol'shaya River, and Kamchatka River basin (Sokol'skaja 1972). On sand and gravel bottoms.

Propappus volki Michaelsen, 1916

Figs. 1, 2b & 3

Palpenchytraeus volki.—Michaelsen, 1916b: (in Michaelsen, 1916a) 1. [nomen nudum].

Propappus volki. Michaelsen, 1916a:51–55; 1923, 37–42; 1926:4.—Cernovitov, 1937b:273, figs. 1–2.—Chekanovskaja, 1962:372–373, fig. 188.—Wachs, 1967:322, fig. 9.—Bird, 1982:67–75. Non Sokol'skaja, 1968:21.

Material examined.—Cotypes from the Cernovitov collection, BMNH 1949.3.1.230, mature, sagittally sectioned specimen, and BMNH 1926.927.1–5, 3 specimens in fluid, collected by W. Michaelsen, in the Lower Elbe River, near Hamburg; Nov 1915 to Jan 1916. Nineteen mature specimens collected from gravel at East Burton on the River Frome, Dorset, England, during period Jan 1979 to Dec 1980. All stained in alcoholic borax carmine. Fifteen specimens subsequently mounted whole in Canada balsam; 3 specimens sectioned transversely and 1 specimen sectioned sagittally, at 7 μm intervals. Twenty mature and 15 immature specimens collected from River Tarn, tributary of Garonne River, Massif Central near Albi, France; 17 Oct 1979. Four specimens attributed to *Propappus volki* from Lake Baikal. Two with developing gonads, one also with developing spermathecae and vasa deferentia. All mounted whole, as above.

Type locality.—Elbe River, near Hamburg, at 3–5 m depth.

Description of material examined.—Four to 7 mm long, with 29, 33–43 segments;

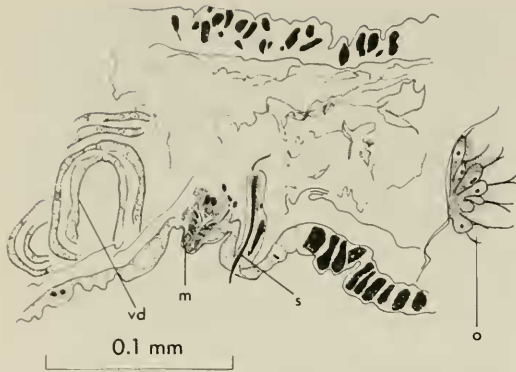


Fig. 3. *Propappus volki*, segment XII with male pore and anterior of XIII with part of an ovarian strand; drawn from a sagittally-sectioned specimen from southern England. Abbreviations—m, male pore; o, ovary; s, seta; vd, vas deferens.

body diameter at IV–V about 150–300 μm , at XI about 300–400 μm ; body of mature specimens usually constricted through XII and XIII. Prostomium with annulate, non-retractile proboscis (Fig. 1a), up to 97 μm long; proboscis with distinct lumen. Setae (Fig. 1a, s; 3, s) 40–80 μm long, ventrals (preclitellar: $\bar{x} = 69.6 \pm 6.7 \mu\text{m}$ [n = 17]; postclitellar: $\bar{x} = 60 \pm 12.4 \mu\text{m}$ [n = 5]) on average just longer than dorsals (preclitellar: $\bar{x} = 64.0 \pm 14.0 \mu\text{m}$ [n = 14]; postclitellar: $\bar{x} = 56.0 \pm 8.0 \mu\text{m}$ [n = 8]); preclitellar setae slightly longer than postclitellar setae; upper tooth much thinner and shorter than lower. Epidermal papillae in transverse ring at level of setae; other epidermal glands in 12–15 transverse rows per segment. Spermathecal pores just posterior to 3/4. Clitellar gland cells small, scattered over XII through $\frac{1}{2}$ XIV. Male pores each on small, conical papilla (Fig. 6, m), body wall usually depressed around papillae. Brain with median, anterodorsal projection. Anterior dorsal blood vessel dividing in front of brain, vessel originating in VII (Fig. 1a, v) or in clitellar segments. Abrupt expansion of gut in VII or XIV to XV. Setal glands (Figs. 1a, s; 2b) flask-shaped, with narrow ectal neck; glands in anterior segments with maximum diameter about 17–25 μm ($\bar{x} =$

20.1 $\pm 3.1 \mu\text{m}$ [n = 10]), about 40–70 μm ($\bar{x} = 57.4 \pm 8.8 \mu\text{m}$ [n = 9]) long. Ectal end filled by large cells with dense, finely or coarsely granular contents. Gland enclosed by cuticle-like layer. Nephridia (Fig. 1b) from 5/6. Seminal vesicle (Fig. 1a, sv) extending as far anterior as VI or VII and posterior into XII. Testes (Fig. 1a, t) large, compact. Vas deferens sometimes with bit of thicker-walled ental part appearing to protrude into XI; ental part 20–52 μm ($\bar{x} = 40 \pm 10 \mu\text{m}$ [n = 15]) in diameter, 154, 171, 186 μm long; ectal part of vas about 7–16 μm ($\bar{x} = 12 \pm 3.4 \mu\text{m}$ [n = 17]) in diameter, widening to 14–23 μm ($\bar{x} = 18.6 \pm 4.2 \mu\text{m}$ [n = 5]) at pore (Fig. 3, m), 2–4 times as long as ental part. Segment XII criss-crossed by muscular strands (Fig. 3). As many as 3 maturing eggs in XIII, extending into XII and/or XIV. Spermathecal ectal duct (Fig. 1a, d) bulbous just ental to pore, 21–29 μm ($\bar{x} = 26 \pm 3.2 \mu\text{m}$ [n = 12]) in diameter at pore to 11–17 μm ($\bar{x} = 13 \pm 1.7 \mu\text{m}$ [n = 12]) between expansion and ampulla. Ampulla (Fig. 1a, a) extending from 4/5 as far as XII, walls very thin.

Remarks.—As for *Propappus glandulosus*, the specimens of *P. volki* held at BMNH are cotypes. The comprehensive description of *P. volki* by Michaelsen (1923) included specimens from the Volga River but none of these could be obtained for this study. The Volga material and additional cotypes are held at the Zoologisches Museum Universität Hamburg.

Discussion.—The ovarian segment in the material examined was always XIII, and there was no evidence for lability of this character in *Propappus volki* (Michaelsen 1916a, 1923).

The origin of the dorsal blood vessel and gut transition in *Propappus volki* are consistently (Michaelsen 1916a, 1923) described as in postclitellar segments, XIV or XV. In the new material from Lake Baikal, none of which was fully mature, an abrupt expansion of the gut (?transition from

esophagus to intestine) was located in VII or VIII, as for *P. glandulosus*, and the dorsal blood vessel origin was at the expansion or just anterior to it. The esophageal wall immediately posterior to the pharyngeal pad was highly folded in all specimens of *P. volki*, perhaps facilitating the eversion of the pad.

In many specimens, the ental part of the setal glands appeared empty. Here the cuticular layer was collapsed forming a "tail" (Fig. 2b) on the gland. The glands appeared to be larger and full in more mature specimens.

The length of the proboscis in specimens of *Propappus volki* obtained from England, France and Lake Baikal varied from 29 μm to 97 μm . Statistical comparisons of the proboscideal length for each population by the *t* test showed that the mean probosces lengths of the French and English populations were not significantly different at the 95% level (mean lengths were 56.2 \pm 11.2 μm [n = 26] and 64.6 \pm 15.9 μm [n = 15], respectively). The mean length of probosces (38.5 \pm 5.4 μm [n = 4]) for Baikal specimens was significantly different from the mean lengths of both French and English populations. The Mann-Whitney U test gave the same results. All mean lengths of probosces were significantly different ($P \ll 0.001$) from a mean of 0 when compared by a *t* test. The presence of a prostomial proboscis may be the only character state that can be used easily to distinguish *P. volki* from *P. glandulosus*. These species differ little in size or in the size and shape of various taxonomic characters including setae, spermathecae and male ducts.

Both *Propappus volki* and *P. glandulosus* are recorded from Lake Baikal. However, *P. glandulosus* is known from only a few additional locations near Lake Baikal, whereas *P. volki* is recorded from numerous, widespread locations in the USSR and Europe.

Distribution. — Widely distributed in western Europe: Germany (Michaelsen 1916a, Stephenson 1930, Wachs 1967);

Austrian Tyrol (Bird 1982); France (Juget 1980, 1984); and northwest Spain (Martinez-Ansemil 1982). Britain, southern England (Ladle and Bird 1980, Bird 1982). Central and eastern Europe: rivers of the Baltic Sea Basin (Parele 1983); Latvia (Cekanovskaja 1962); Estonia (Bird 1982); Ukraine and Moldavia (Grigelis 1980); Poland: Tatra and Carpathian Mountains (Bird 1982), Welna and other Polish rivers (Kasprzak 1980); Czechoslovakia (Bird 1982); and Romania (Bird 1982). Central USSR: large rivers, especially Volga and tributaries, and reservoirs (Michaelsen 1923, 1926; Cekanovskaja 1962; Grigelis 1980; Bird 1982); Lakes Baikal, Chud and Pskov (Cekanovskaja 1962). In springs and phreatic waters (moving ground waters); small stony streams, on sand beds in large rivers, in the sandy substrates of lakes and reservoirs (Bird 1982).

Propappus arhyncotus Sokolskaja, 1972

Propappus arhyncotus Sokolskaja, 1972:83–85, fig. 5; 1973:64–66, fig. 8.

Propappus volki. — Sokolskaja, 1968:21.

Type material. — No. 1001 in the Zoological Museum of Moscow University (not seen). Collected 11 Aug 1964 by V. Ya. Lavanidov.

Type locality. — Kamchatka, Lake Azabach'e at 7 cm depth; gravel substrates.

Description from the literature. — Six to 12 mm long, maximum diameter 300–400 μm ; with 29–40 segments. Prostomium large, without proboscis. Setae commonly 3–4, rarely 5–6 per bundle in preclitellar segments, usually 3 posteriorly. Dorsal setae 55–71 μm long, ventral setae 59–76 μm long; length of setae increasing slightly from anterior to posterior segments; upper tooth much shorter and thinner than lower; nodulus distal. Spermathecal pores approximately lateral at or in 3/4. Small epidermal tubercles irregularly distributed on prostomium and peristomium, in more regular rings in following segments. Male pores on

cone-shaped papillae. Setal glands flask-shaped, about $55\ \mu\text{m}$ by $27\ \mu\text{m}$ at segments VII–X. Most anterior nephridia in V (? at 5/6). Esophagus widening to intestine at XV. Vasa deferentia about $310\ \mu\text{m}$ long, widening from about $17\ \mu\text{m}$ in diameter entally to $29\ \mu\text{m}$ near pore, distal end further widened to $34\text{--}38\ \mu\text{m}$ but with narrow channel. Ovaries paired in anterior of XII. Spermathecal duct about $160\ \mu\text{m}$ long, extending through IV, ampulla may extend into VI.

Remarks.—It has not been possible to borrow or otherwise obtain specimens of *Propappus arhyncotus*, and some questions concerning its structure could not be resolved.

Discussion.—Sokolskaja (1972) recorded that bundles of three through six setae were present; however, she consistently depicted (1972, fig. 5A, obviously schematic) only three setae per bundle. Other species of *Propappus* have only two or three setae per bundle. As in some enchytraeids, replacement setae may be present at the same time as the seta or the bundle being replaced. This was observed here in *P. volki*. The entire bundle complement can be replaced simultaneously, leading, in *Propappus* species, to bundles appearing to have four or six and possibly five setae.

The condition of the male duct described by Sokolskaja (1973) for *Propappus arhyncotus* is quite different from that found in either *P. volki* or *P. glandulosus*. In the former the vas deferens widens from the ental to the ectal end whereas in the latter two species the ental part (about one-quarter of the total length of the vas deferens) is notably wider and the walls more "glandular" than in the ectal part. In *P. arhyncotus* there is a considerable widening of the vas deferens at the male pore, to about $34\text{--}38\ \mu\text{m}$. In *P. volki* and *P. glandulosus* the terminal part of the vas deferens is either not measurably wider or may be a few micrometers wider than the ectal part, with a maximum diameter of $23\ \mu\text{m}$ in *P. volki*.

It was originally stated (Sokolskaja 1972), and has been confirmed (Sokolskaja, pers. comm.) that the ovaries are in segment XII in *Propappus arhyncotus*. It would seem that little doubt could remain about this character state. However, the same character state has erroneously persisted in the literature regarding both *P. glandulosus* and *P. volki* for more than 60 years. Other shared characters point to a very close relationship of all three species and similarity of the gonadal condition seems probable.

Sokolskaja (1972) pointed out four categories of differences of *Propappus arhyncotus* from *P. volki*: 1) the shape of the prostomium and absence of proboscis; 2) the thickness and sculpturing of the cuticle; 3) the location of the spermathecal pores in 3/4; and 4) the structure of the spermatheca, with a short ampulla extending only into V. Michaelsen (1923) mentioned that the cuticle in *Propappus* was very thick and that there were rings of prominent epidermal cells around the segments. The epidermal papillae are similarly described by Sokolskaja (1972). The location of the spermathecal pore in all the specimens of *Propappus* examined was in or very near the furrow marking 3/4. Sokolskaja (1973) modified the description of the spermatheca of *P. arhyncotus* to indicate that the ampulla was more sac-like and extensive in mature specimens. Apparently only the proboscicial (and ovarial) character state separates *P. arhyncotus* from *P. volki*.

Propappus arhyncotus was distinguished (Sokolskaja 1972) from *P. glandulosus* by the postclitellar location of the esophageal-intestinal transition in the former. This is a character that may be difficult to determine without examination of the cellular structure of the gut. In much of the fixed material examined here the location of the gut transition was, in fact, difficult or impossible to observe. Present estimations of the location of the gut transition are not consistently reliable.

This species remains a systematic prob-

lem. If the ovaries are in XIII, then *Propappus arhyncotus* probably should be synonymized with *P. glandulosus*. However, the condition of the male ducts also requires examination. If the ovaries are in XII, *P. arhyncotus* may differ from the other species of *Propappus* at the generic or even familial level. Only re-examination of specimens of *P. arhyncotus* can resolve its specific, generic and familial relationships and consequent classification.

Distribution.—Kamchatka Peninsula: Zhupanova River basin, inflow of Bol'shaya River, Kamchatka River basin, including Lakes Azabach'e and Klyuchevskoe.

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